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The distribution of southern African Harpagophoridae Attems, 1909 (Diplopoda: Spirostreptida)

by

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ABSTRACT

The southern African Harpagophoridae comprises three genera: *Zinophora* (12 described and four undescribed species), *Harpagophora* (six described and one undescribed species) and *Poratophilus* (three species, including one unconfirmed species). Recent collecting in South Africa, and taxonomic revisions, have provided new insights facilitating a biogeographical study. The family is widely distributed within the subregion, and at altitudes up to 1600 m. The distribution of *Harpagophora* and *Zinophora* is non-overlapping and is strongly linked to rainfall seasonality and biome, with *Harpagophora* being confined to winter rainfall, and to Succulent Karoo and Fynbos biomes, while *Zinophora* mainly occurs in the summer rainfall Savannah and Grassland biomes, with a few species in Thicket and Nama Karoo. Both of these genera can be divided into distinct species–groups based on gonopod morphology, and these groupings also have a clear geographic basis. The distribution of individual species appears to be linked to biomes, and more widespread species occur in extensive biomes such as Savannah. Barriers which have isolated or separated genera, species–groups, and individual species, are difficult to determine, but rivers and altitude may be important factors limiting distribution and promoting vicariance.

INTRODUCTION

Millipedes generally tend to have rather localised distributions and individual species seldom occupy an extensive area. Those that are found in many parts of the world all owe their wide distribution to commercial activities such as the importation of plants and soil (Lawrence 1984). The distribution of millipedes is influenced by a variety of factors acting at different levels. There have been several attempts to examine the global distribution of millipedes and to link this to plate tectonics and continental drift (Hopkin & Read 1992). Millipedes are quite conservative in their ecological requirements (Kime & Golovatch 2000), and most species have a strong dependence on humid microclimates (Hopkin & Read 1992), and on soil which is not too dry or compacted for burrowing (Lawrence 1984). Limitations are also imposed on their geographical dispersal into dry areas by the long periods required for moulting, during which they are vulnerable to desiccation (Lawrence 1984). These special requirements favour isolation, and as a result, millipedes have a strong tendency to speciate (Hopkin & Read 1992), and species are generally confined to relatively small areas.

The biogeography of invertebrates is an under-researched field, particularly in Africa (Hamer & Slotow 2000). Some of the factors contributing to this are the lack of taxonomic knowledge and the great shortage of expertise in the region. The millipede fauna of Africa generally is poorly known, but that of South Africa was considered by Hoffman (1985) to be relatively well known. However, a recent revision of the large-bodied and conspicuous species of the spirostreptid genus *Doratogonus* resulted in the description of 15 new species (Hamer 2000), increasing the known diversity in the genus by 43 %.

A revision of the southern African Harpagophoridae has just been completed (Redman 2003), and this enables an investigation into biogeography of this family in the subregion.

The Harpagophoridae is the second smallest family of the order Spirostreptida in southern Africa, following the Julomorphidae. Our knowledge of the family in the subregion largely results from the contributions of Brandt (1841), Karsch (1881), Silvestri (1897), Attems (1909 1914 1928 1934), Carl (1917), Chamberlin (1927), Kraus (1958), Schubart (1966), Lawrence (1938 1965 1984), Hoffman (1994), Demange (1961 1983), Hoffman & Golovatch (1998) and Hamer (1998).

In Africa, the Harpagophoridae are represented by the following genera: *Poratophilus* Silvestri, 1897, *Harpagophora* Attems, 1909, *Zinophora* Chamberlin, 1927, *Apoctenophora* Hoffman & Howell, 1982 and *Obelostreptus* Krabbe, 1982. *Apoctenophora* and *Obelostreptus* range from Tanzania north to Ethiopia (Hoffman & Howell 1982). In southern Africa, the family currently comprises three genera and a total of 26 confirmed species (Redman 2003): *Harpagophora* (seven species), *Zinophora* (16 species) and *Poratophilus* (three species), with only *Zinophora* being represented beyond the Zambezi and Kunene Rivers, in the Democatic Republic of Congo (formerly Zaire) and Tanzania. The recent revision of the southern African harpagophorid fauna has resulted in several taxonomic changes, the description of five new species, and the identification of a new genus (Redman 2003).

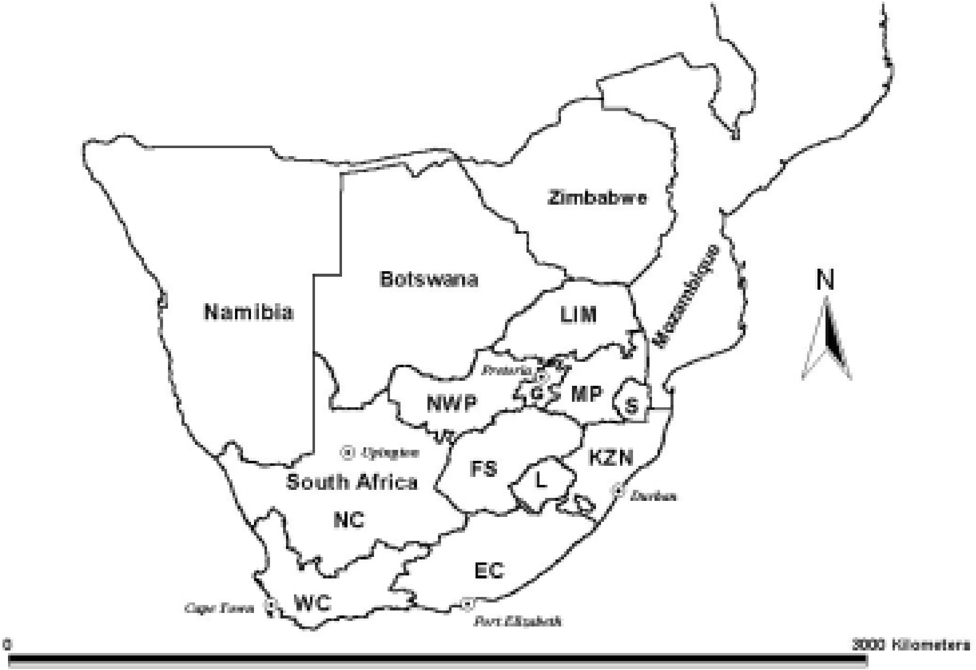


Fig. 1. Map of southern Africa showing countries, provinces and major cities. Abbreviations: Provinces: WC = Western Cape; EC = Eastern Cape; KZN = KwaZulu-Natal; MP = Mpumalanga; LIM = Limpopo; NC = Northern Cape; NWP = North West Province; G = Gauteng; FS = Free State. Countries: L = Lesotho; S = Swaziland.

The objectives of the present study were to determine the overall distribution of the Harpagophoridae in Africa south of the Zambezi and Kunene Rivers (Fig. 1); to investigate possible factors influencing the distribution of the family, genera, species and species-groups; and to identify factors that may have contributed to isolation and speciation in the different taxa.

METHODS

In total 245 specimen lots of Harpagophoridae were examined from the collections of the Natal Museum, Iziko Museum (South African Museum), Northern Flagship Institute (Transvaal Museum), Albany Museum, National Museum (all in South Africa), and from the Virginia Museum of Natural History (United States of America), and the Museum für Naturkunde der Humboldt Universität (Germany).

Spatial analysis

All male specimens were identified to species. Locality information for recently collected material was entered into a spatially referenced Microsoft Access®© database using Global Positioning System readings. Older localities were estimated to the nearest minute on 1:250 000 scale maps. The Access data were exported into ArcView®© GIS (Environmental Systems Research Institute) and patterns of distribution were examined with reference to base maps or coverages with biotic and abiotic environmental features. Coverages of vegetation types and biomes were obtained from Low & Rebelo (1996), and altitude was obtained from Schulze *et al*. (1997). All locations for the family were

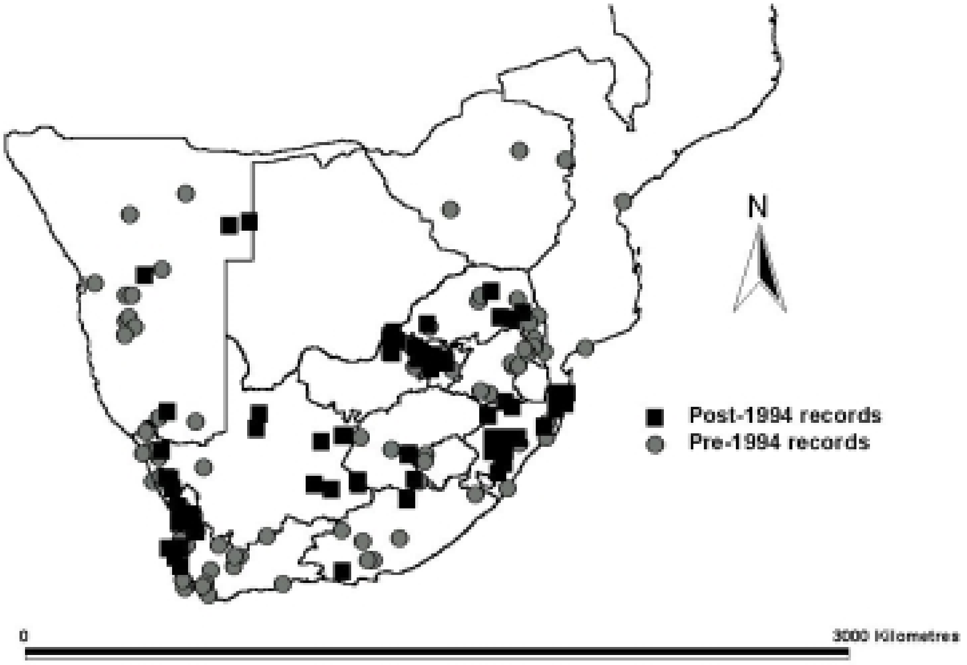


Fig. 2. Collection localities for harpagophorids in southern Africa before and after 1994.

superimposed onto coverages to look for any possible barriers or factors influencing the distribution of the family, genera and species. These included major river systems, changes in vegetation type or biome, and rainfall patterns. The data for all the coverages were only for South Africa; species occurring beyond the borders were not included in the analysis.

Only those species considered valid by Redman (2003) have been included in the analysis. This means that the following synonymies or generic allocations, although **not** yet formally proposed, are used here in accordance with ICZN 4, Article 8.3: *Julus* (*Spirostreptus*) *gracilis* (Brandt, 1841) = *Zinophora gracilis*; *Harpagophora levis* Attems, 1928 = *Zinophora levis*; *H. polyodus* Attems, 1909 = *H. alokopyga* Attems, 1909; *Z. robusta* (Attems, 1928) = *Z. munda* Chamberlain, 1927; and *Z. minor* (Lawrence, 1938) = *H. attenuata* (Brandt, 1841).

RESULTS

Surveys and distribution of the family

Figure 2 illustrates the rapid increase in the number of harpagophorid samples collected after 1994. About 47 % of the total number of records post-date 1994. This was the result of concerted efforts to address the lack of collecting in the two largest biomes in South Africa, namely Savannah and Grassland. A pioneer South African myriapodologist, the late R. F. Lawrence (Natal Museum) had focussed his collecting in South African forests, from which harpagophorids are absent.

Figure 3 illustrates the wide distribution of harpagophorids. They occur across southern Africa from the east to the west coast, and from the Cape Peninsula to the

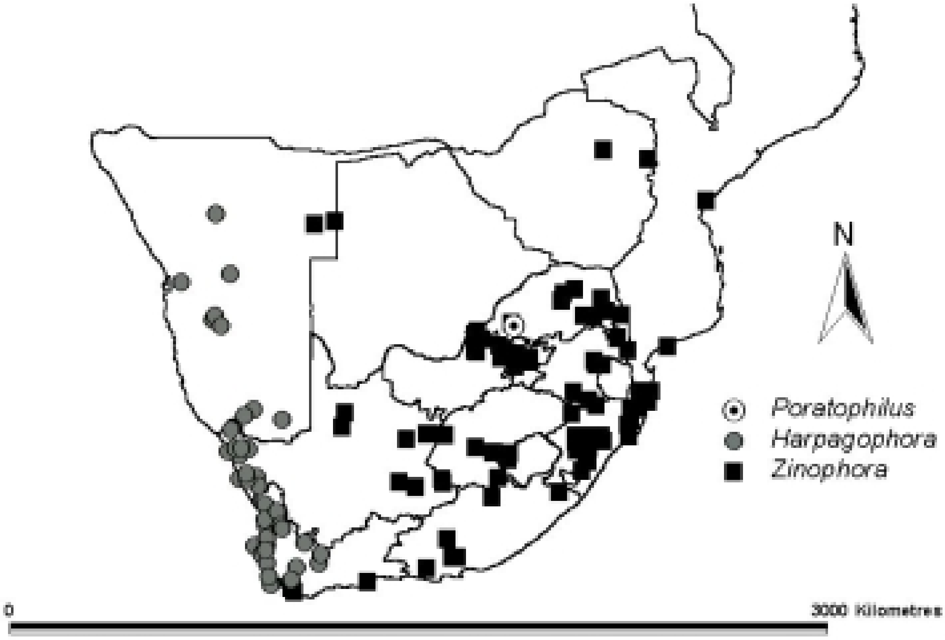


Fig. 3. Distribution of harpagophorid genera in southern Africa.

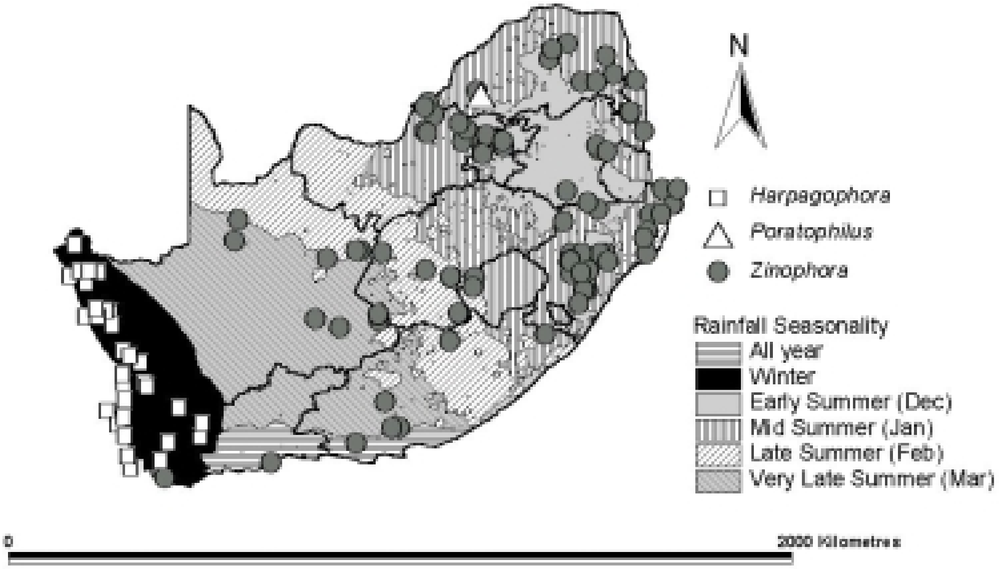


Fig. 4. Distribution of harpagophorid genera relative to rainfall seasonality (winter, summer rainfall regions) in South Africa.

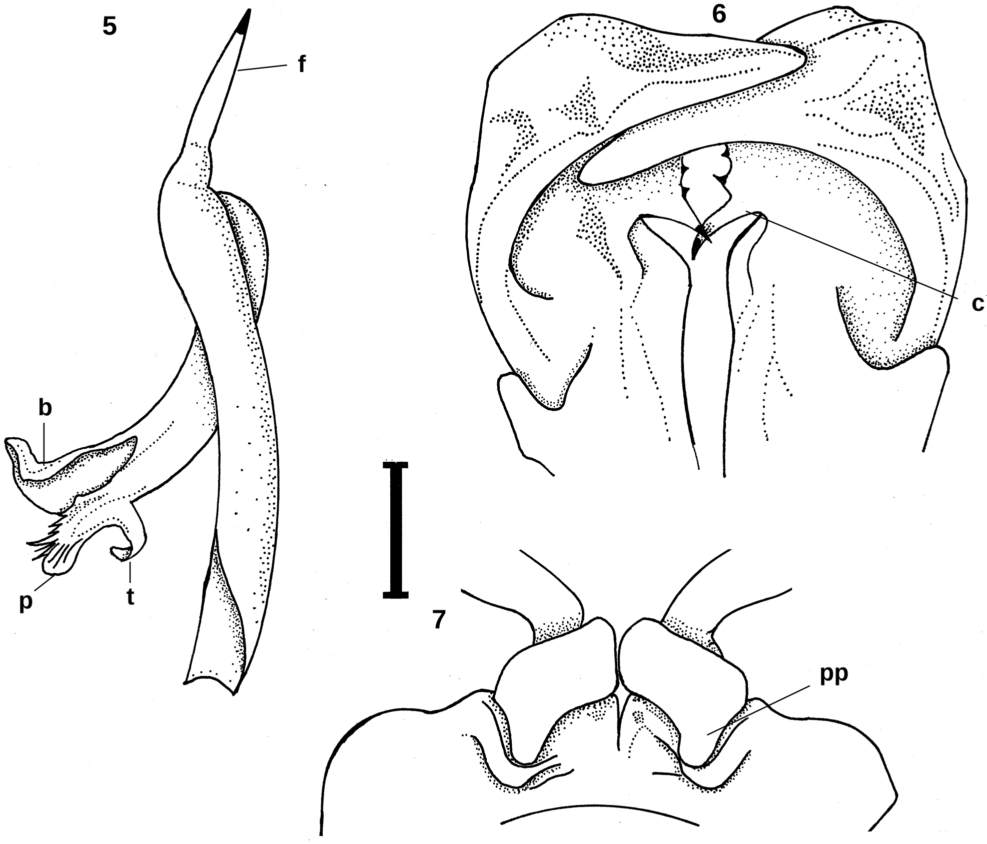
most northern parts of the region in Zimbabwe and Namibia. The family is thus represented in the arid west of the subregion and in the wettest east, in the low lying areas along the coast on the high-altitude central plateau, and even in the Drakensberg mountain range at about 2300 m. They are also present in six of the seven broad biomes, or vegetation types in South Africa, with only forest lacking any harpagophorid records.

Large gaps in the distribution are probably a collecting artefact, rather than an actual absence of the family. This is especially true for Mozambique and Botswana.

Distribution of the genera

The two larger genera of Harpagophoridae occurring in South Africa have a non-overlapping distribution (Fig. 3). *Harpagophora* is confined to the Western and Northern Cape provinces and Namibia. *Zinophora* has a wider distribution, more concentrated in the eastern and central parts of South Africa. *Poratophilus* has been confirmed from only a single locality in the Waterberg range of the Limpopo Province (*P. gorteri*). The source of the type species (*P. australis* Silvestri, 1897) is ‘South Africa’, and a third species (*P.* (*P.*) *mokhotlongensis* Schubart, 1966) was described from a female specimen only, and its generic identity cannot be confirmed.

The distribution of the genera appears to be correlated with biomes (Figs 8, 13 & 21) and a combination of rainfall seasonality (Fig. 4), quantity and reliability. In South Africa *Harpagophora* is confined to the winter rainfall, Fynbos and Succulent Karoo biomes (Figs 4, 21). *Zinophora* occurs in the Grassland and Savannah, and less extensively in the Nama Karoo where rainfall is predominantly during the summer months (Figs 4, 8 & 13). In addition to seasonal change, the quantity and reliability of



Figs 5–7. *Zinophora* Group A. 5–6. *Zinophora similis*. 5. Telopodite. 6. Aboral view of gonopods. 7. *Z. diplodonta*, 1st pair of male legs, oral view. b = second lamella; c = telocoxal spine; f = femoral spine; p = pectinophore; pp = prefemoral process; t = thumb. Scale = 1 mm.

rain decreases towards the west coast. Only one *Zinophora* species occurs in the winter rainfall parts of the south-east coast. The amount of annual rainfall alone appears to have little influence on the distribution of the genera, with both *Harpagophora* and *Zinophora* occurring in arid areas and in those with over 600 mm per annum.

Species-groups

Both *Harpagophora* and *Zinophora* can be divided into two distinct species-groups based on morphology, predominantly of the gonopods. These divisions are correlated with the distribution of the groups.

In *Zinophora*, the species in Group A share a narrow incurved thumb on the telopodite, a lobed median margin of the posterior telocoxal fold (Figs 5–7), and an elongate, finger-like process on the prefemur of the first pair of legs in the male (with the exception of *Z. junodi* (Carl, 1917)). *Zinophora sabulosa* (Attems, 1928), *Z. brevilobata* (Attems, 1928), *Z. laminata* (Lawrence, 1965), *Z. diplodonta* (Attems, 1928), *Z. munda* Chamberlain, 1927, *Z. similis* (Carl, 1917) and *Z. junodi* are grouped here.

Group B includes those species that share a saucer-shaped thumb (i.e. concave) on the apical elements of the telopodite, a bluntly and weakly produced median margin of the posterior telocoxal fold (Figs 9–12), and the first pair of male legs without prefemoral processes. The group is further divided into subgroups: B_1 and B_2. In the five species of B_1 (*Z. gracilis*, *Z. brevispina* (Lawrence, 1965), *Z. punctata* (Attems, 1928), *Z. ochropygialis* (Schubart, 1966) and *Zinophora* sp. n. 1), the ozopore series begins on the fifth segment, and all the species have a single femoral spine. In B_2 species (*Z. levis*, *Zinophora* spp. n. 2, 3 and 4) the ozopore series begins on the sixth segment, three of the species have two femoral spines, and one has a single femoral spine.

The three *Zinophora* species-groups are geographically distinct. Group A species are limited to the northern parts of southern Africa, from north-eastern KwaZulu-Natal, through Mpumalanga, and westwards through the North West Province into the Northern Cape. The distribution of this group appears to be strongly linked to biome, with records predominantly in Savannah, with just two species also occurring along the fringes of the Savannah and Grassland biomes (Fig. 8). In Group B_1 the species are distributed from the Western Cape north-eastwards to the Free State and Lesotho, while B_2 is confined to the eastern side of the Drakensberg Escarpment in KwaZulu-Natal and Mpumalanga (Fig. 13). The exact localities for *Z. ochropygialis* in the Western Cape have not been confirmed and are based on the original description. This is the only species of Group B that occurs only in Fynbos habitat. The remainder of the species occur in Grassland, Thicket or Nama Karoo habitat. *Zinophora punctata* is unusual in that the other species appear to be confined to a single biome, but this species occurs in Nama Karoo, Thicket and Fynbos. In B_2 three species occur in a combination of Grassland, Savannah and Thicket biomes, while the fourth species (*Zinophora* sp. n. 4) is known only from high-altitude grassland (Fig. 13).

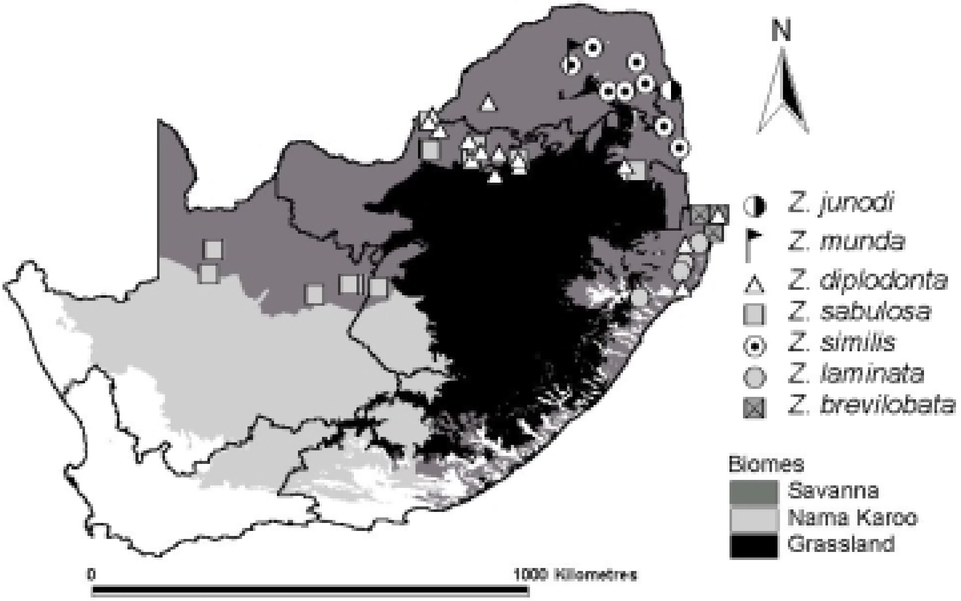
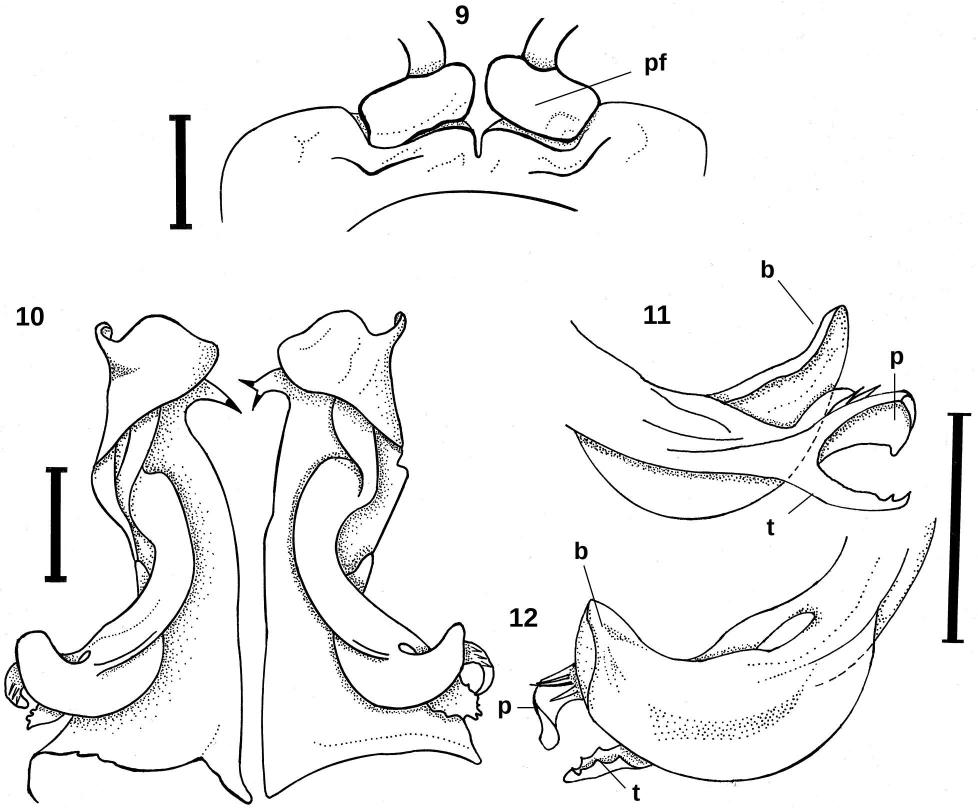


Fig. 8. Distribution of *Zinophora* Group A species relative to the Grassland and Savannah biomes.



Figs 9–12. *Zinophora* Group B. 9. *Zinophora levis*, 1st pair of male legs, oral view. 10–12. *Zinophora mudenensis*. 10. Aboral view of gonopods. 11. Apical elements of telopodite, oral view. 12. Apical elements of telopodite, aboral view. b = second lamella; p = pectinophore; t = thumb; pf = prefemora. Scales = 1 mm.

The *Harpagophora* species in Group C (*H. monodus* Attems, 1909, *H. dittoktenus* Attems, 1914, *H. alokopyga*, and *H. attenuata*) share very similar distal ends (apical elements) of the telopodite of the gonopods (Figs 14–16). Group D species (*H. diplocrada* Attems, 1909 and *Harpagophora* sp. n. 1) can be distinguished from Group C species by the apical elements of the telopodite, as well as by the posterior corner of the collum which has a protuberance overlapping the second segment and a reduced caudal spine (Figs 17–20). In addition, these species are generally larger and more robust than the species of Group C.

Group D has only been recorded in Namibia and Group C has only been recorded in South Africa in the Western and Northern Cape along the west coast (Fig. 21). Namibia and South Africa are separated by the Orange River. The two Group D species occur in an extension of the Succulent Karoo biome in southern Namibia, through to the dwarf shrub Savannah to the highland and thornbush Savannah (*H. diplocrada*) in central Namibia. These biomes are not indicated on the map.

Harpagophora spirobolina (Karsch, 1881) does not resemble any of the other species of *Harpagophora* closely, and may represent a new genus. It occupies the same habitat as some of the Group C species (Fig. 21).

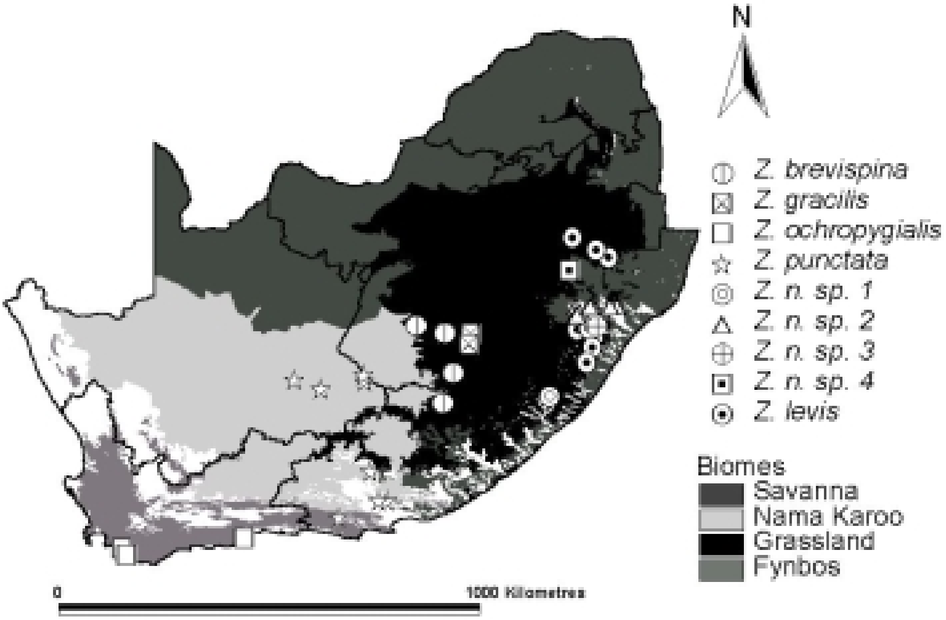


Fig. 13. Distribution of *Zinophora* Group B_1 and B_2 relative to biomes in South Africa.

Species distributions

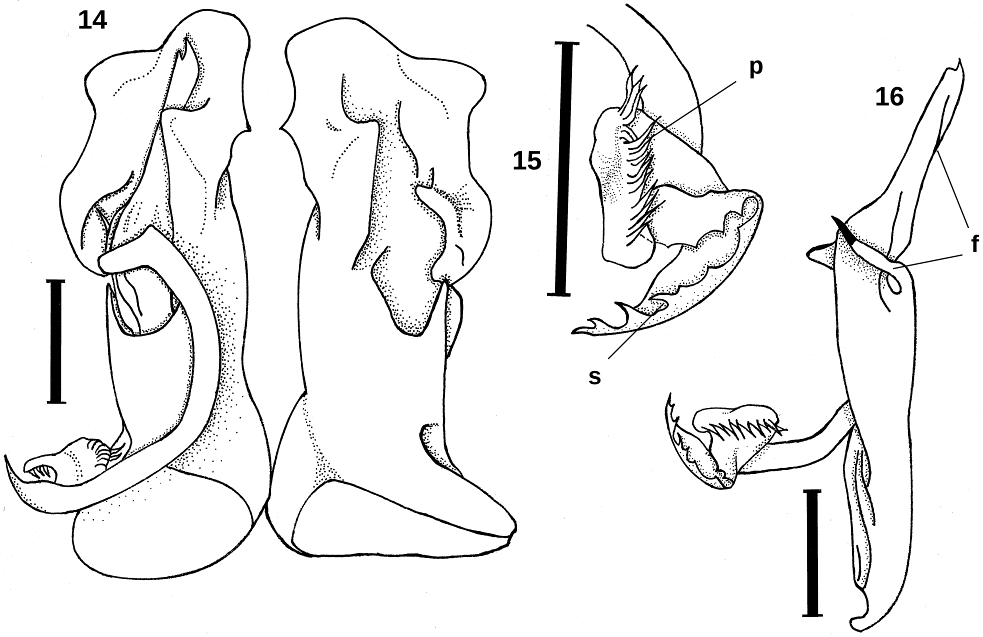
Most harpagophorid species have a relatively limited distribution, and six species (*P. gorteri*, *P.* (*P.*) *mokhotlongensis*, *H. dittoktenus*, *Zinophora* spp. n. 1, 3 and 4) are each known from a single locality. The distribution of individual species appears to be confined to vegetation type or biome, the size of which also seems to affect the extent of occurrence of the species. The most widely distributed species are those that occur in Savannah habitats. For example, *Z. sabulosa* occurs in northern Namibia and across a wide band through the northern parts of South Africa (Fig. 8). Other relatively widely distributed species occurring in the Savannah biome are *Z. diplodonta*, *Z. similis*, *Z. laminata* and *Z. munda* (Fig. 8). Two of the species that are known from single localities (*Zinophora* spp. n. 1 and 4), occur in high-altitude grasslands (Fig. 13), and *Zinophora* sp. n. 3 is confined to the Tugela Valley where Thicket biome is represented (Fig. 13).

Species richness distribution

KwaZulu-Natal and the Western Cape both have the highest levels of species richness, with seven (27 % of the total number of species) and six (23 %) species respectively. The other provinces of South Africa are less speciose, with Mpumalanga having four species, Gauteng and the Eastern Cape each with three species, Limpopo and the North West Provinces with two species each, and the Free State with one species.

DISCUSSION

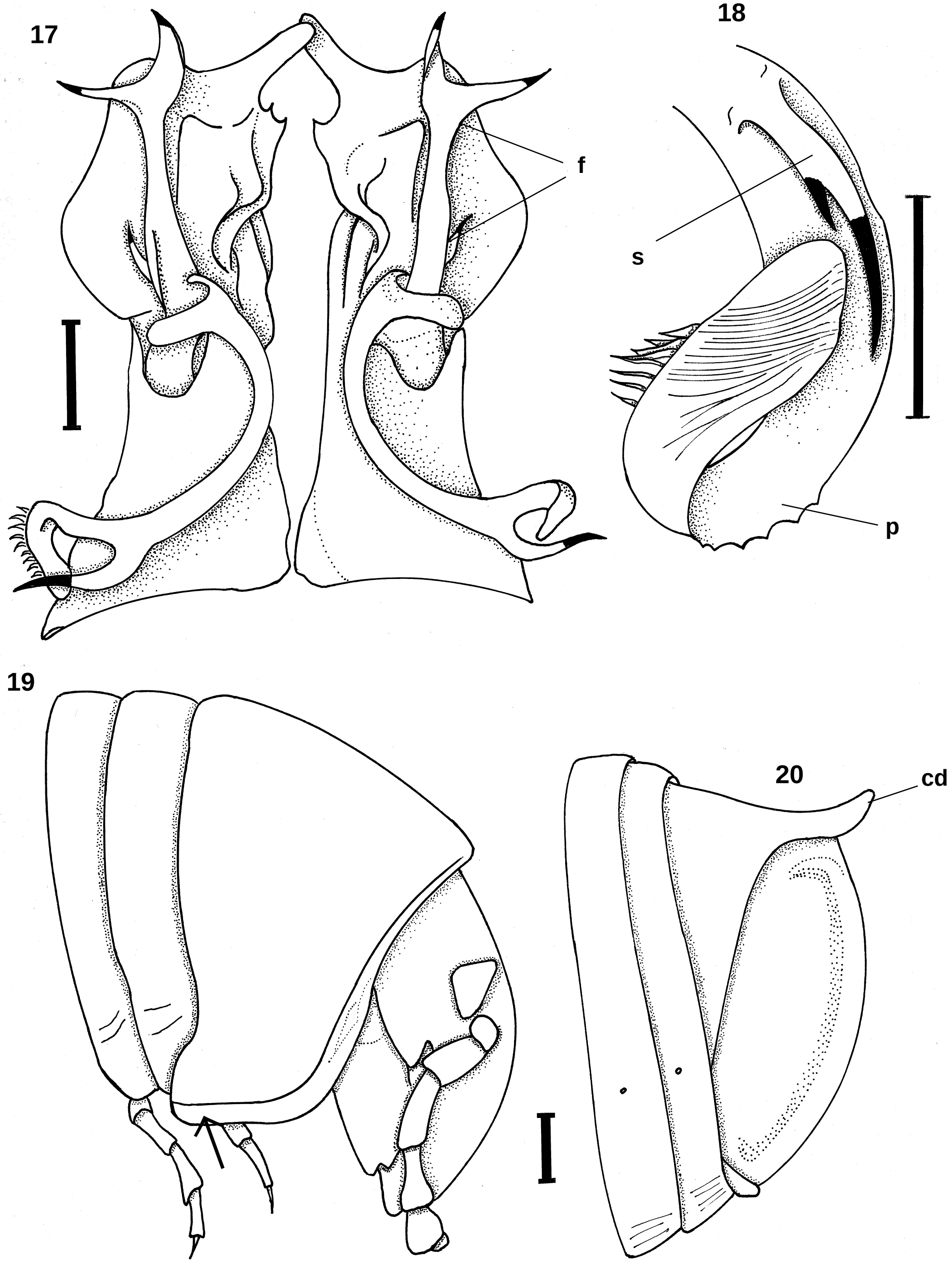
Although the millipede fauna of southern Africa can be considered well known relative to that of the rest of Africa (Hoffman 1985), enormous gaps in taxonomic and biogeographic knowledge still exist. This is illustrated by the southern African



Figs 14–16. *Harpagophora* Group C, *Harpagophora alokopyga*; 14. Aboral view of gonopods. 15. Apical elements of telopodite (oral view). 16. Telopodite (oral view). f = femoral spine; p = pectinophore; s = spine branch. Scales = 1 mm.

harpagophorids, whose taxonomic revision revealed five new species (an increase of 23 %), several species allocated to the incorrect genus, new synonymies, a possible new genus, and the identification of previously undifferentiated species-groups (Redman 2003). In addition, the distribution of the family, genera and several species was shown to be much broader than previously perceived. Future study, especially of new collections from outside South Africa, will probably result in an increased diversity for the family, and in new distribution records, which could result in a different interpretation of biogeography from that discussed here. At this stage, however, biogeographic patterns in South Africa do appear to be discernible.

The family has a wide distribution in southern Africa, ranging from semi-desert environments in Namibia to the moist KwaZulu-Natal north coast, and from the lowland areas along the coast to the high-altitude Drakensberg at about 2300 m. Rainfall seasonality, rather than annual amount, generally appears to influence distribution. This is understandable given that millipede surface activity is strongly seasonal (Dangerfield & Telford 1991; Telford & Dangerfield 1993). This may however not be true for the western part of the Northern Cape, where quantity and reliability of rainfall may also play a role. Biome or vegetation type probably has the most obvious influence on the distribution of genera, species-groups and individual species. The close association between harpagophorid distribution and biomes is evident in Figures 8, 13 and 21. There is also a clear correlation between the extent of a biome and the extent of the distribution of genera and species. The *Zinophora* Group A is the most widely distributed group in southern Africa, and similarly, the Savannah biome in which it



Figs 17–20. *Harpagophora* Group D. 17. *H. diplocrada*, aboral view of gonopods. 18. *Harpagophora* sp. n. 1, apical elements of telopodite. 19–20. *H. diplocrada*. 19. Note posterior lateral margin of collum overlaps second segment (indicated by arrow). 20. Caudal spine reduced. p = pectinophore; s = spine branch; cd = caudal spine. Scales = 1 mm.

occurs (Fig. 8) is the largest biome in southern Africa, occupying 46 % of the area of the subregion and over 33 % of the area of South Africa (Low & Rebelo 1996). The Thicket, Succulent Karoo and Fynbos biomes are the smallest biomes in which harpagophorids occur in South Africa, and similarly the genera and species occurring in these areas have more restricted distributions than those in the Savannah (Figs 13, 21). A similar trend was evident in *Doratogonus* in southern Africa (Hamer & Slotow 2000). In this genus, those species that occur in Savannah have wide distributions, while those species restricted to Forest, a small and patchily distributed biome in South Africa, have localised distributions.

Speciation amongst forest millipedes in South Africa is likely to have been allopatric through vicariance. Forests became fragmented and reduced in size during glacial maxima, leading to isolation of populations of millipedes. Forest expanded and became continuous again during interglacials (Lawes 1990). This resulted in groups of closely related species in the genus *Doratogonus* (Spirostreptidae) along the lowland areas of the eastern seaboard of South Africa (Hamer & Slotow, 2000). Understanding vicariance and isolation events in taxa in more widely distributed and continuous biomes such as Grassland and Savannah is not so easy.

The historical biogeography of harpagophorids is unclear. In the southern African harpagophorids, mountain ranges and rivers appear to separate species-groups and, to a

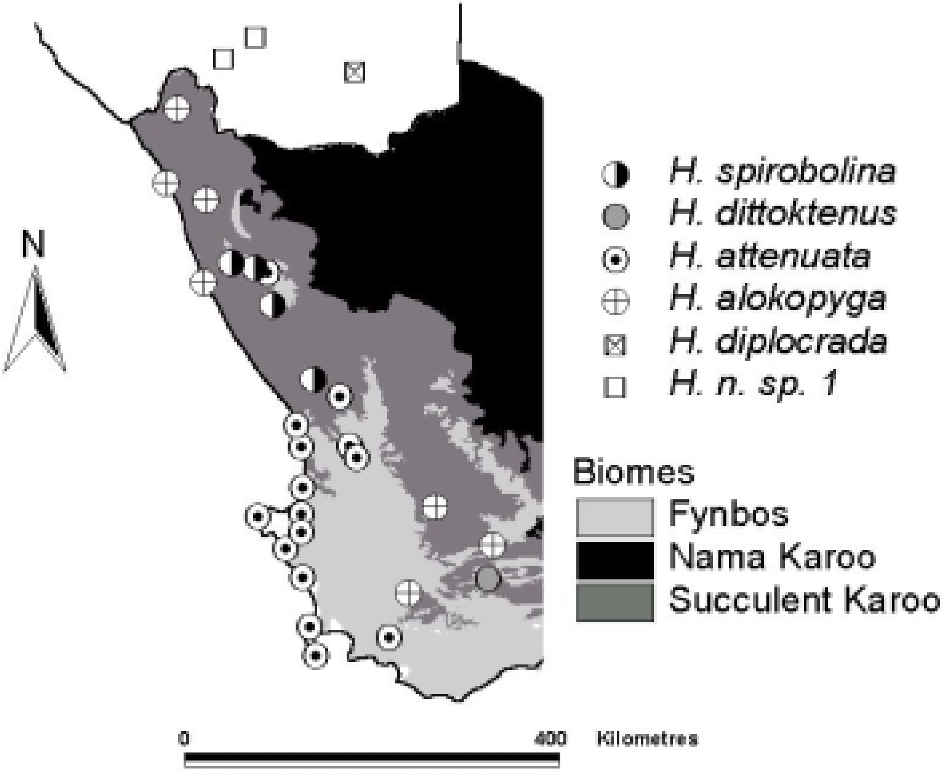


Fig. 21. Distribution of *Harpagophora* Group C and Group D in Namibia and South Africa, with biomes in South Africa shown.

lesser extent, species. However, the same barriers often separate biomes with which species or species-groups are tightly associated. It is therefore not clear whether the biogeographic role of mountains and rivers is ecological or historical.

The value of investigation of distribution patterns at various taxonomic levels became evident through this study. *Harpagophora levis* had only been recorded from the summer rainfall area east of the Escarpment (Fig. 13). The confinement of the other members of this genus to the west coast, winter rainfall region raised suspicions regarding the relationships of *H. levis*. This led to a re-examination and re-evaluation of the generic characters. *Harpagophora* had previously been separated from *Zinophora* by the presence of two femoral spines as opposed to one. It became evident that the form and size of these spines, rather than number, were important generic characters, and that there were other characters useful in characterising the genera. In a future publication *levis* will be transferred to *Zinophora*.

The present study has illustrated the value of investigating distribution at different taxonomic levels for enhancing understanding of taxonomy and species relationships. The study also has conservation implications through highlighting those species which may have small ranges, and which are therefore more threatened through habitat alteration.

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